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FURTHER STUDIES ON THE ACTIVITIES OF ARANEADS[1]

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1. AGE DIFFERENCES IN THE SNARES OF TWO ARGIOPIDS

To the best of my knowledge there has been made no comparison of the snares of immature and adult spiders, with regard to the problem of whether such snares become more complex as the animal grows older. Yet this is an interesting question in its bearings upon the perfection of an activity through repeated effort.

During the past months of July and August I have studied this matter on two common species of argiopids, *Epeira sclopetaria* (Clerck) and *E. marmorea* (Clerck), both of which construct large vertical, orbicular snares that are very favorable for measurements and the architecture of which has been well described by McCook.[2]

My observations were made at Woods Hole, Mass., where there was a large colony of *sclopetaria* in the laboratory buildings and beneath the boat wharves, and another of *marmorea* in a marshy woodland. All the webs measured were those in the free and natural conditions, except those of the newly hatched; to obtain the latter I kept cocoons until they hatched, then freed the young upon the window panes of my room where they spun their first snares. *Sclopetaria* makes cocoons throughout

[1] Contributions from the Zoological Laboratory of the University of Pennsylvania.

[2] American Spiders and their Spinning Work, Philadelphia, 1889–93.

the summer, and one female under observation furnished four successive ones (all made in the night); they hatch on the twenty-fifth or twenty-sixth day. *Marmorea* does not construct cocoons until the fall. Comparisons were made on the following points: (1) number of radii, (2) number of spiral loops, (3) greatest diameter of the spiral (orb proper). The spiral loops examined are those of the outer viscid spiral which is the true trap of the web, and the number of its turns were counted in that segment of the orb where they were most numerous (generally in the region below the central hub). A slight error is sometimes encountered in counting these loops for occasionally the innermost of them are scarcely distinguishable from the inner non-viscid spiral, but this is an error of only small amount.

The following table gives in condensed form the measurements of 265 snares. On the left is entered the species, sex and age, the linear measurements are in centimeters, the remainder is self-explanatory.

	Radii			Spiral Loops			Snare Diameter		
	Number of Counts	Extreme Numbers	Average Number	Number of Counts	Extreme Numbers	Average Number	Number of Counts	Extreme Sizes	Average Size
E. marmorea:									
♀ ♀, adult	87	19–43	28.3	87	29–71	48.2	86	18.5–48.3	28
♀ ♀, penultimate instar	19	21–35	27.8	19	16–61	48	19	16.5–35.6	23.4
♂ ♂, penultimate instar	16	23–36	28.3	16	26–61	41.3	16	14 –30	20.6
♂ ♂, antepenultimate instar	3	19–34	27.3	3	37–39	38	3	19.6–25.4	22.1
Young from .3–.6 cm.	23	19–35	28.7	23	16–51	29.5	21	7.6–28	15
E. sclopetaria:									
♀ ♀, adult	24	15–24	19	21	26–56	35.4	24	24.1–48.3	35.6
♂ ♂, penultimate instar	2	18–23	20.5	2	24–30	27	2	20.3–30.5	25.4
Newly hatched	91	11–20	15.3	91	11–23	16.2	91	5.1–11.9	7.6

With regard to increase of complexity of the snare with advance of age of the spider this table shows us the following figures for *sclopetaria*. The first formed snares, those of the newly hatched, exhibit an average of 15.3 radii, 16.2 spiral turns and 7.6 cm. diameter in comparison with averages of 19. radii, 35.4 spiral turns

and 35.6 cm. diameter of adult females. In other words while the diameter of the orb increases nearly five times, the number of spirals becomes slightly more than doubled, and the number of radii are increased less than one quarter. For *E. marmorea* the webs of immature individuals of from .3 to .6 cm. were compared with those of adult females, and the table shows that between these ages the number of radii remains about constant, while the number of spiral turns and the diameter of the spiral about double themselves; females in the penultimate instar show the orb almost as complex as that of females in the last instar.[3] For both of the species examined, accordingly, the age changes in the snare are greatest with regard to the diameter of the viscid spiral, less with regard to the number of its loops (on the average these only doubling their number), and least with regard to the number of the radii.

It is interesting that the first snare of the spiderling has all the parts of that of the adult, namely, the central woven hub and the inner non-viscid spiral in addition to the viscid spiral, radii and foundation lines. With increasing age of the spider the threads of the snare become thicker, the whole structure larger, but otherwise beyond the addition of a few more radii and a doubling of the number of the spiral turns there is no particular change effected. The newly-hatched show also about the same specific habits as do the adult: in *marmorea* the young, as does the mother, remains in a nest in a curled leaf holding communication with the snare only by a trap-line; and in *sclopetaria* the young, again like the mother, remains either at the center of the snare or else away from it, holding a trap-line but not hiding within a nest. Further, though there are frequently imperfections in the snares of the young, such as incomplete radii, asymmetri-

[3] By last or ultimate instar is meant the one of sexual maturity, even though this may be, and in some species regularly is, followed by other moults; the penultimate instar would be the next preceding, and the antepenultimate the one before that.

cally placed spirals and imperfect meshing of the hub, such imperfections seem to be quite as usual in adult webs so that it is rare in either of these species to find perfectly symmetrical webs. The adult spider can not be said to construct a more serviceable snare than does the spiderling, for the spiderling's is really much larger in diameter in proportion to the size of the body. And while the adult has about twice as many spiral loops, the spiderling with his fewer loops probably secures all necessary nourishment to the same extent as does his mother. Thus with the growth of the spider the snare does not become more serviceable as a trap. In all this excellent architecture the young as well as the adult labors first to make a scaffolding to support its weight, then lays down upon this the food-gathering spiral; and it does this quite as efficiently as does the adult. We might conclude that the number of spiral loops becomes larger because the supply of available silk has greatly increased; and that more radii are added because the weight of the spider increases faster than the size of the web, and because the spider in all her building tests the strength of the scaffolding, adding a new line wherever the structure sags. But the increase in number of parts can not be ascribed to intelligence, or memory of reiterated experience, for the mother seems to continue the same instinct possessed by the young and shows no peculiarity in the spinning process not exhibited by the latter. The age differences of the web are, accordingly, due mainly to: (1) increase in the weight of the spider in combination with the instinct to make the scaffolding sufficiently strong; and increase of size of the spinning organs, therefore of silk substance. The spider does not exhibit learning at any stage, for it constructs the first web with as much ease and certainty as any later one. In this connection I may also mention, as the result of many observations, that the spider makes the first cocoon as perfectly as any subsequent cocoon; and when it makes a mistake at any part of the process of cocoon spinning seems unable to rectify it.

The absolute size of the snare and the number of spiral loops vary much in individuals of the same species. The size is dependent upon two factors: (1) size of the space in which the web is spun, and (2) amount of silk available. If confined in a cramped place the spider spins no snare at all, as I found by attempting to induce them to spin in cages made of two panes of window glass separated by a wooden rim 3 cm. thick. Then if successive webs are destroyed soon after making each contains fewer parts than its predecessor, which can be ascribed only to deficiency of silk. Thus with one adult female of *sclopetaria* her first snare had 21 radii, 35 spiral loops, and a diameter of 37 cm.; this I destroyed, and her second made a day or two later had 17 radii, 25 spiral loops and a diameter of 30.5 cm.; a week later I destroyed this and she made a third with 18 radii, 25 spiral loops and diameter of 24.1 cm., then (after demolition of this one) a fourth with 19 radii, 19 spirals and diameter of 23 cm.

In orbs of adult females, particularly of *marmorea,* the space between neighboring spiral loops varies greatly in size, whence it follows that the diameter of the orb is no index of the number of spiral turnings, and that different females must use different parts of the body as a measure of this space. This is really the most marked variation to be found in orbs, and it is shown just as well in those of spiderings.

2. The Snares of Male Argiopids and the Number of Males

In this conjunction I wished to compare the spinning activities of males of *Epeira marmorea* and *E. sclopetaria* with those of their females. On this matter McCook has to say:[4]

> As a rule, the spinning abilities of male spiders, as far as they relate to the capture of prey, have been shown in Volume I to be less decided than with females. The rule is not absolute for all species, as in some cases the snare spun by the male is precisely like that woven by

[4] *L. c.,* 2, p. 65.

the female. But in certain other genera, as, for example, Argiope and probably Nephila, the snares of the male are rudimentary, and do not compare in perfection with those of the female.

The immature males of the two species studied by me construct perfect snares of the types of those of their respective females. But the adult males of *marmorea* (no adult males of *sclopetaria* were examined) do not spin snares at all but build nests near those of adult females and live on the outskirts of the snares of the latter; this was the case with all of the 23 mature males found in the latter half of the month of August.

Data on the snares of immature males are condensed in the table already presented. The snares of orbs of 16 males of *marmorea* in the penultimate instar show the same average number of radii, a somewhat smaller average number of spiral loops (41.3 to 48), and a smaller average diameter (20.6 cm. in comparison with 23.4 cm. and 28. cm., as compared with snares of females of this species in the penultimate instar and at maturity. Data for the snares of 3 males in the antepenultimate instar show somewhat lower averages. Those of 2 males of *sclopetaria* in the penultimate instar, show, on comparison with adult females of this species, a slightly greater average number of radii (20.5 to 19), a smaller average of spiral turns (27 to 35.4), and a smaller average diameter (25.4 cm. to 35.6 cm.). That is to say, males in their penultimate instar construct fully as many radii as do females in their penultimate or even ultimate instar, but a smaller number of spiral turns and they make smaller snares. But a male in his penultimate instar is considerably smaller than a female of the same age, therefore in proportion to his size and weight his snare is quite as complicated as that of the female and is in no sense rudimentary. It would appear, accordingly, that the spinning instinct, so far as the snare is concerned, is as perfect in the male as in the female. He makes no web when mature because the sexual impulse completely overcomes the desire for food, hence the instinct for snaring it, though

he does continue to construct nests; and his nest is quite as complex as that of the female. I have not determined whether a male after satisfaction of his sexual desires would again spin a snare; but probably he would not have a chance of doing so, for the female becomes satisfied before he does and frequently succeeds in devouring him. Indeed, I have obsrved a female of *marmorea* devouring one male while another was importunely making advances to her.

As to the sexual ratio of *mormorea,* I found in the field 16 males of the penultimate instar to 19 females of the same age, and 23 adult males to 87 adult females. These figures are too meager to allow of any general conclusion, beyond that the males at maturity seem to be less than half as numerous as females, and just before maturity to be slightly less numerous. The greater disparity in numbers at maturity may well be due to accidents befalling males while they are seeking mates and to their destruction by the females themselves. On August 31 I measured the orbs of 24 adult females of *marmorea;* on only 8 of them were there adult males, these webs having from one to three males each. It is probable that more than one male copulates with a given female, and that a given male may mate with more than one female; for I have found this to be the case with *Theridium tepidariorm* and certain Lycosids.[5]

3. The Senses of Touch and Sight in Snare-making Spiders

The number of eyes in araneads, usually eight, their different positions upon the head area, and their complexity in being compound (constructed of separate retinulae), has led naturalists to the view that the sense of sight plays a large part in their vital activities. And this idea is substantiated for such species as are strictly hunt-

[5] Before the antepenultimate instar males can not be distinguished externally from females. According to W. Wagner (La Mue des Araignées, *Ann. Sci. Nat.,* 1888) the external male peculiarities do not exhibit themselves in *Attus* before the fifth moult, and in *Lycosa* before the seventh.

ers and not snarers, and particularly for the diurnal Attidae as demonstrated by the studies of the Peckhams.[6] But among the snare-weavers I feel positive, in agreement with McCook's conclusions, that the sense of touch almost completely supplants that of sight. Long observation in the field and especially upon species kept under control has led me to this opinion, the main reasons for which may be briefly mentioned. The lines of the snare are the medium by which the spider secures its food and conducts its mating, all by touch. In the operation of spinning, whether it be a snare or a nest or a cocoon, the process is conducted beneath the ventral surface of the spider, accordingly, in a position removed from its field of vision; and all such architecture is frequently carried on in the dark of night. With the true orb-weavers, the argiopids, the spider sometimes remains at the center of the orb holding tensely with its tarsal claws various radii and thereby feeling any object that strikes the web. In this position she can see only a small part of the snare, if any of it, yet she instantly perceives any impact upon any part of the snare. Or the spider does not rest upon the snare at all, or comes out upon it only at night and twilight, remaining in a nest at some distance from the snare; in that case the spider perceives any shock to the snare by means of the trap-line that passes from her claws to the center of the snare, such a trap-line being a modified radius. McCook (*l. c.*) has given an admirable treatment of the use of this trap-line and of how it is often employed to spring the snare. Thus *Epeira marmorea* remains through the hours of sunshine for the most part in a nest within a leaf that has curled up, where she can not see the web at all, and feels every motion of it through the connecting trap-line. And it is instructive to watch her when an insect agitates the snare. She then rapidly pulls the trap-line several times, thereby learning that the prey is struggling in the web, runs

[6] Peckham, G. W. and E. G. Sense of Sight in Spiders. *Trans. Wisconsin Acad. Sci.*, 1894.

rapidly to the center of the snare, then locates the insect precisely by pulling successively different radii. In this food-gathering she seems to use touch alone, and it is questionable whether she at any time sees her food, for even in the process of mastication and sucking she holds it beneath her head. And this sense of touch is so delicate that by it the spider can to some extent determine the nature of the object that causes the impact, as, *e. g.*, whether it be large or small.

Likewise with the mating, that I observed this summer in *Epeira marmorea*. The female was near the center of her snare hanging vertically downward with her dorsal surface, her vision area, away from the male. He was at the outer end of one of her radii and though his head was turned towards her he perceived her position and tested her inclinations not by sight but by touch communicated through that radius; they signalled to each other by pulls and counter pulls of the line, he climbed along the radius towards her, at nearly every step repeating his pulling, then when about an inch away he advanced rapidly to press his palpi against her epigynum while she drew in her extremities close to her body. Each such act was only of momentary duration, and at its end he moved away along the same radius, repeated his signalling, then again advanced towards her; thus there were numerous repeated copulations during the half hour I watched the pair.[7] The female never saw the male at all, and he perceived her so far as I could determine by the sense of touch alone. In an earlier study, where I

[7] Previous observers of European species of this genus have described this process in much the same way. Compare:

Walckenaer. Histoire naturelle des Insectes. Aptères. Suites à Buffon, 2, Paris, 1837.

Menge, A. Ueber die Lebensweise der Arachniden. *Schriften naturf. Ges. Danzig*, 4, 1843.

Menge. Preussische Spinnen, I. *Ibid.* (N. F.), 1, 1866.

Termeyer, R. M. de. Researches and Experiments upon Silk from Spiders, etc. Translated by Burt G. Wilder, *Proc. Essex Inst.*, 5, 1866.

Lendl, A. Ueber die Begattung der gekrönten Kreuzspinne (*Epeira diademata* Cl.). *Termész. Fuzetek, Budapest*, 10, 1886.

described this act in much greater detail for various other species,[8] I had called attention to this exclusive use of touch in the courtship and copulation of snare-weavers. The female responds to the male's signals by more gentle and weak pulls when she is eager for him, by stronger and more aggressive ones when she regards him as an object of food; thus there is a language of touch, even at a distance, and the male assures himself, if such an expression is permissible, of the nature of his partner's responses. In the case of *marmorea* just described the male took effective means to procure his escape should the female prove aggressive, just as did the male of *E. diadematа* observed by Menge: while advancing along her web radius he held an escape line of his own, the outer end of which was attached to the periphery of her web; and when her motions were more violent than usual he loosed his hold on her radius to drop and swing out of her reach on his own escape line. In this way he procured the double advantage of escape and of remaining in communication with her web.

It may be noted in passing that while in *E. marmorea* the male seeks only adult females, in *Theridium tepidariorum* the males mature somewhat earlier than the females and are to be found upon the webs of the females before the latter have matured.

We can say that among araneads the sense of touch is the dominant one in those that are snarers. Spiders lack hearing, as seems to be proved by the experiments of my student Miss Pritchett.[9] The long spines placed upon the limbs seem to be tactile and not auditory organs. Spiders possess the olfactory sense but it is not known how much they are guided by it. The primary sense of the snarers is touch, and they possess it to a

[8] Studies on the Habits of Spiders, particularly those of the Mating Period, *Proc. Acad. Nat. Sci. Philadelphia,* 1903.

[9] Pritchett, A. H. Observations on Hearing and Smell in Spiders. AMER. NAT., 38, 1904. These observations have been criticized by F. Dahl (*Naturwiss. Wochenschr.*, N. F., 4, 1905), but Dahl never instituted crucial experiments such as those of Miss Pritchett.

degree of perfection hardly equalled by any other terrestrial animals.

The question then presses, of what use are the eyes to snare-weavers when their sensations are so particularly tactile? The newly hatched spiderlings evidently use their eyes for they are always positively phototropic while the adults are generally negatively so. This turning towards the light benefits the spiderlings and consequently the species by serving to disseminate them from the home area into new feeding grounds. And I believe it is a quite general phenomenon among all animals whose adults are more or less sedentary and tubicolous, negatively phototropic, for the young to be at first positively phototropic, though I do not know whether any one has drawn attention to the comprehensiveness of this principle; in this most wide-spread kind of migration the beneficial result of the change of tropism is to prevent overcrowding. But as the young snare-weaver grows older and begins to avoid the light as does its parent, it does not employ its eyes in the primal acts of feeding and mating but mainly determines by them the source of the light in order to avoid it. Despite their complexity, accordingly, the eyes of snare-weavers, when they have passed infancy, seem to be used mostly as direction eyes. This being the case it seems strange that these eyes should have retained the complexity inherited from hunting forefathers, and it is possible that they have come to subserve some other new function, as, *e. g.,* to have become thermic receptors; this might well be determined experimentally. At any rate we shall have to change current views as to the rôle of vision in spiders.

4. On the Average Duration of Life in Araneads

In the case of all species that I have studied adult males are found during only a short period of the year, for perhaps not longer than a month or six weeks, and in latitudes where there is a marked winter season they do not live over this period of cold. And from observations on *Theridium tepidariorum* I estimate from the rate

of growth that this species is able to reach full size in one year. Males, accordingly, live for only a relatively short time as adults, and their life time would seem to not exceed one year. In my observations on *Epeira marmorea* I found on July 25 among 16 recognizable females (in young of 8 mm. body length or less the sexes are externally indistinguishable) only 5 adults, while on August 31 out of 24 females all but 3 were adult; these data indicate for this species that while at the beginning of the summer few females are adults, at its end most are. It is then probable for this species, though not proved, that few females live over from one breeding season to another, and then only under favoring environmental conditions, a conclusion reached by McCook for *Argiope*. But the females live at least some months longer than the males for they are to be found later than the breeding season and after all males have disappeared; and there are cases on record (cf. McCook) where females of certain species have been kept from two to seven years. I have described for *Latrodectus*[10] how the mating occurs in the late winter at Austin, Texas, the adult males are not found after this season, while the females continue to produce cocoons until the following autumn. We might say in general that males of spiders probably do not live longer than one year, females some months longer or in certain cases several years.

5. THE COCOONING OF LOXOSCELES RUFESCENS DUF

I give these brief notes here because the cocooning of no sicariid has been hitherto described, and because it may be of some interest from the standpoint of comparative architecture. The cocoon of *Loxosceles* is sessile, attached to the snare, so resembling that of *Sicarius,* while in *Scytodes,* the only other genus of the Sicariidae for which the cocoon has been described, it is carried in the chelicera of the mother.[11]

[10] *Jour. Exper. Zool.,* 5, 1908.

[11] I have taken these genera as defined by E. Simon: Histoire naturelle des Araignées, 2me éd., Paris, 1892.

This is an abundant form at Austin, Texas, where it makes a large and irregular web beneath logs and stones, usually in drier situations. In its movements it is the most languid and timid species I have ever seen, waiting quietly until its prey has inextricably entangled itself in the web, and feigning death for a remarkably long period. Both males and females are able to undergo thirst for weeks at a time, an unusual faculty among spiders, and to this ability it probably owes its success under the desiccating Texan sun.

On June 13, 1907, I placed six females in separate glass cages. Four of them when first found had each a single cocoon, and each produced cocoons in captivity to the number of from two to four each. One of them produced five cocoons in all.[12] The season of cocooning evidently extends through the whole three months of the summer.

The cocoons are discoidal, with diameter longer than the spider's body, and are made in the mornings from seven o'clock to noon. In the two cases where the operation was observed they were spun against a vertical wall of the cage, not placed horizontally. After making the base, a process not seen, the spider remains quietly above it until the following day, a cessation of activity quite unique among araneads but thoroughly in accord with *Loxosceles's* quiet disposition. Then the eggs are laid upon this base, an act that occupied eight minutes in the case where it was followed. Over the egg mass the mother spins a thin-textured cover, swaying the spinnerets leisurely back and forth; this cover spinning occupied one hour in the case where it was timed. The mother remains upon the cocoon until it hatches.

[12] Some naturalists write as though multiple cocoons were a rather exceptional phenomenon among spiders. On the contrary I believe it is the general if not universal rule, for I have found it to be the case also in lycosids, pisaurids, attids, agalenids, thomisids, clubionids, drassids, theridiids, argiopids, dictyniids and filistatids.